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A NEW SPECIES OF *CHROTOMYS* (RODENTIA: MURIDAE) FROM LUZON ISLAND, PHILIPPINES

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Abstract.—A new species of *Chrotomys* (*C. gonzalesi*) is described from Mount Isarog on the Camarines Peninsula of southeastern Luzon Island, Philippines. It is one of four species of murid rodents confined to high elevation forest on this mountain. The new species is distinguishable from congeners by its relatively lower braincase, broader mastoid region, broader palate, and darker pelage. Data suggest that the new species is semifossorial, active both day and night, and feeds on annelid worms and soft-bodied arthropods. This discovery supports a general pattern of vicariant speciation between the highlands of northern and southern Luzon.

The murid rodent fauna of northern Luzon Island in the Philippines is a spectacular example of ecological and morphological radiation in isolation. Oldfield Thomas (1895, 1898) first described this remarkable fauna, which includes such diverse species as: *Phloeomys pallidus,* the arboreal giant cloud rat; *Rhynchomys soricoides,* the long-snouted shrew-rat; and *Chrotomys whiteheadi,* a species noteworthy for its pelage marked by a unique pattern of prominent dorsal stripes. Additional information on *Chrotomys* did not appear until a half-century later, when Kellogg (1945) named the subspecies *C. whiteheadi mindorensis* based on one specimen from southwestern Mindoro Island. Subsequently, Musser et al. (1982) examined additional specimens from Luzon and Mindoro and recognized two species, *Chrotomys whiteheadi* from the highlands of northern Luzon and *C. mindorensis* from lowland regions in southern Mindoro and central Luzon.

The diverse Philippine fauna, with its attendant potential for furthering our understanding of evolutionary dynamics of archipelagic communities, is severely threatened by habitat destruction. In the Philippines as a whole, primary forest cover has been reduced from more than 80% of total area at the turn of the century to about 8% currently (Myers 1988). Our current studies address evolutionary biogeography, patterns of diversity, and conservation biology of Philippine mammals (e.g., Heaney 1986, Heaney & Heideman 1987, Heaney & Rickart 1990).

To these ends, between March and May 1988, we surveyed mammals in Mount Isarog National Park on the Camarines Peninsula of southeastern Luzon Island (Rickart et al. 1991). Rising to 1966 m and surrounded by lowland plains, Mount Isarog is an extinct volcano that is the highest and most isolated forested peak in southern Luzon (Goodman & Gonzales 1990). This isolation evidently has led to the development of a distinctive mammal fauna. In 1961, an expedition to the mountain, led by D. S. Rabor of Silliman University, obtained a small collection of murid rodents that included the new genus and species *Archboldomys luzonensis* (Musser 1982) and the new species *Rhynchomys isarogensis* (Musser & Freeman 1981). During our 1988 survey, we obtained eight examples of a third species of *Chrotomys* that we name and describe in this report. The diagnosis of the

Mount Isarog *Chrotomys* is placed in the context of comparisons to *C. mindorensis* and *C. whiteheadi,* and to *Celaenomys silaceus,* the presumed sister-group of the genus *Chrotomys* (Heaney & Rickart 1990).

Specimens Examined and Methods

Specimens examined in this study are deposited at the American Museum of Natural History, New York (AMNH), Field Museum of Natural History, Chicago (FMNH), Bell Museum of Natural History, University of Minnesota, Minneapolis (MMNH), and United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The following comparative samples were used: *Chrotomys whiteheadi* (6).—LUZON: Mountain Province, Mount Data region (AMNH 18513; FMNH 62281, 62282; USNM 102547, 102548, 102552); *Chrotomys mindorensis* (10).—LUZON: Laguna Province, Los Baños, International Rice Research Institute (USNM 536800–536802); Nueva Ecija Province, San Jose, south of Manikla (USNM 399581); Pampanga Province, Clark Air Base (USNM 356390); Tarlac Province, San Miguel, Concepcion (USNM 349048–349050); MINDORO: Mindoro Occidental Province, 3 mi, SSE San Jose, Central (USNM 277639, holotype); Mount Iglit Station (MMNH 12972); *Celaenomys silaceus* (2).—LUZON: Mountain Province, Mount Data region (FMNH 62286, 62287).

External measurements were recorded from specimen labels or from field notes of collectors. If external measurements were missing, length of hind foot (including claws) was measured from fluid-preserved specimens or study skins. Thirty-nine cranial, mandibular, and tooth dimensions, recorded to the nearest 0.1 mm using dial calipers, were measured on adult specimens, and tooth measurements were taken on young specimens with fully erupted permanent dentition. Limits of measurements follow the protocol of Musser (1979), with the following exceptions: condylobasal length—anterior edge of premaxilla to posterior margin of occipital condyle; palatal length—anterior edge of premaxilla to posterior margin of bony palate; mastoid breadth—greatest width across mastoid processes; condylar breadth—greatest width across occipital condyles; breadth of braincase—least width immediately behind zygomatic arches; orbital length—most anterior point in orbit to most posterior point on inner margin of zygomatic arch in temporal fossa; breadth of nasals—greatest width across nasals; length of rostrum—anterior edge of premaxilla to most anterior point in orbit; depth of rostrum—anterior edge of incisive foramina to nearest point on dorsal surface of nasals; palatal breadth—greatest width across crowns of maxillary toothrows; length of mandibular toothrow—alveolar length from anterior margin of m1 to posterior margin of m3; length of lower incisor—anterior margin of incisor alveolus to incisor tip (not along curve); length of mandible—greatest length from anterior margin of incisor alveolus to posterior edge of condyle; height of mandible—greatest height from coronoid process to angular process; depth of mandibular ramus—alveolus at middle of m1 to nearest point on ventral edge of mandible; size of molars—greatest length and width of crowns of each upper and lower molar.

Student's *t*-test was used to assess differences between group means for cranial and external measurements. To provide a general quantitative description of cranial and mandibular variation among specimens, principal components analysis was performed on log-transformed measurements using the correlation matrix. Data were analyzed by Statistical Analysis System programs (SAS Institute, Inc. 1985) on a desktop microcomputer.

Results

Chrotomys gonzalesi, new species
Figs. 1–2

Holotype.—USNM 458952, adult male collected on 28 April 1988 (original number 4176 of L. R. Heaney); skull with carcass preserved in fluid. The right occipital region of the skull is slightly damaged, otherwise the specimen is in excellent condition. The holotype is currently deposited in the USNM but will be transferred to the Philippine National Museum, Manila.

Type locality.—Western slope of Mount Isarog, 4 km N, 21 km E Naga, Camarines Sur Province, Luzon Island, Philippines, 1350 m elevation, 13°40′N, 123°22′E.

Distribution.—Known only from primary forest on the western slope of Mount Isarog, between 1350 and 1750 m elevation.

Referred specimens.—In addition to the holotype, there are seven other specimens (USNM 458951, 458953–458958) collected during March and April 1988, on the western slope of Mount Isarog between 1350 and 1750 m elevation. Five of these consist of skulls with carcasses in fluid, and two are whole carcasses in fluid.

Etymology.—Named in honor of Pedro C. Gonzales of the Philippine National Museum, in recognition of his devotion to the study and conservation of Philippine birds and mammals.

Diagnosis.—A medium-sized rat (mean weight of adults 136 g) similar to other *Chrotomys* in size and general body proportions (Table 1). Distinguishable from *C. mindorensis* by its generally darker dorsal coloration, less prominent medial stripe, proportionately shorter tail, proportionately smaller plantar pads, lower braincase, broader mastoid region, broader palate, shorter and thinner mandible, and longer lower incisors. Distinguishable from *C. whiteheadi* by its darker dorsal coloration, broader and deeper rostrum, lower braincase, broader mastoid and interorbital regions, broader palate, larger auditory bulla, and larger molariform teeth.

Description.—*Chrotomys gonzalesi* (Fig. 1) has the general morphology of a semi-fossorial rodent. The body is stout and cylindrical, with short, strong limbs and large forefeet armed with strong claws. Pelage is soft, dense, and fluffy; hairs average 15 mm long mid-dorsally. Predominant dorsal color from snout to tail is shiny black, with faint brown highlights. Individual hairs are bicolored, with basal one-third dark gray and the remainder black. In most specimens a pale yellowish buff medial stripe extends from the forehead to the base of the tail. In others the stripe is faint, discontinuous, and confined to the head and upper back. Hairs comprising the medial stripe are similar to those of adjoining black areas, but have pale tips 2–3 mm long. Mid-lateral pelage also is yellowish buff, darker over the shoulders and flanks. Transition between lateral and dorsal color is gradual, and there is no sharp transition between the color of the sides and underparts. Underparts are dark gray, faintly washed with grayish buff, particularly at the sides. Three specimens have a white blaze along the midline on the chest or upper abdomen. Aside from the region of the medial stripe, the top of the head is blackish to the snout. Lips are silvery gray blending to yellowish buff on the cheeks and side of head. Mystacial vibrissae are blackish gray. There is no eye ring. Pinnae are pale gray, nearly naked on the anterior surface but with a sparse covering of short gray hairs on the posterior surface. Dorsally, the metapodials are dark gray, covered with short dark hairs. Digits are pale and naked. The fore feet are relatively large, and are modified for digging. With the exception of the pollex, the digits are long and strong, the longest being the third. The pollex has a short, thick nail, whereas the other digits bear long, thick, nearly straight claws. The palmar surface is naked and unpigmented, with three small interdigital and two large metacarpal pads.

Table 1.—Cranial, dental, and external measurements of *Chrotomys gonzalesi, C. whiteheadi, C. mindorensis,* and *Celaenomys silaceus.* Probability statements are for equality of means for *C. gonzalesi* as opposed to *C. whiteheadi* (P1), *C. mindorensis* (P2), and *Celaenomys* (P3), respectively.

	Chrotomys gonzalesi						
		Total sample			*Chrotomys whiteheadi*		
Measurement	Holotype	Mean ± *SD*	Range	*n*	Mean ± *SD*	Range	*n*
Condylobasal length	41.9	39.8 ± 1.9	38.7–41.9	3	40.4 ± 1.1	39.3–42.0	4
Diastema length	15.8	14.8 ± 0.9	14.0–15.8	4	14.9 ± 0.5	14.3–15.5	5
Incisive foramina length	4.0	4.1 ± 0.3	3.9–4.5	4	4.7 ± 0.2	4.5–5.0	5
Incisive foramina breadth	2.3	2.1 ± 0.1	2.0–2.3	4	2.2 ± 0.1	2.1–2.3	5
Palatal length	23.1	22.1 ± 1.1	21.0–23.1	4	22.2 ± 0.6	21.4–23.2	5
Post-palatal length	15.9	15.2 ± 0.5	14.8–15.9	4	15.5 ± 0.5	14.8–15.8	4
Length of bulla	5.8	5.8 ± 0.1	5.7–5.9	5	5.4 ± 0.2	5.2–5.7	5
Mastoid breadth		13.2 ± 0.2	13.0–13.4	3	12.2 ± 0.3	11.9–12.6	5
Condylar breadth		10.1 ± 0.4	9.8–10.5	3	9.7 ± 0.3	9.6–10.0	5
Height of braincase	11.5	11.5 ± 0.1	11.3–11.6	5	11.8 ± 0.2	11.6–12.1	3
Breadth of braincase	15.7	15.9 ± 0.1	15.7–16.0	4	15.7 ± 0.2	15.5–15.8	3
Zygomatic breadth	22.4	21.4 ± 0.8	20.4–22.4	4	21.7 ± 0.3	21.5–22.0	3
Interorbital breadth	7.7	7.8 ± 0.1	7.7–7.9	5	7.3 ± 0.2	7.1–7.5	4
Orbital length	14.6	13.7 ± 0.7	12.8–14.6	5	13.4 ± 0.7	12.7–14.1	4
Length of nasals	13.6	13.0 ± 0.6	12.2–13.6	4	12.7 ± 0.4	12.3–13.2	5
Breadth of nasals	3.8	3.7 ± 0.2	3.4–3.9	4	3.6 ± 0.3	3.2–3.9	5
Length of rostrum	18.1	17.4 ± 0.7	16.8–18.1	4	17.6 ± 0.4	17.1–18.1	5
Breadth of rostrum	8.8	8.4 ± 0.3	8.1–8.8	4	7.9 ± 0.2	7.6–8.2	5
Depth of rostrum	8.0	7.6 ± 0.3	7.4–8.0	4	7.2 ± 0.2	7.0–7.4	5
Zygomatic plate breadth	3.3	3.1 ± 0.2	2.9–3.3	5	3.1 ± 0.2	3.0–3.3	5
Maxillary toothrow length	6.0	6.2 ± 0.2	6.0–6.4	6	5.6 ± 0.2	5.3–5.7	4
Palatal breadth	8.1	8.1 ± 0.1	8.0–8.3	5	7.2 ± 0.3	7.0–7.7	5
Mandibular toothrow length	6.5	6.5 ± 0.1	6.4–6.6	6	5.6 ± 0.3	5.5–6.0	5
Lower incisor length	9.6	9.6 ± 0.4	9.1–10.1	5	9.5 ± 0.7	8.5–10.2	5
Length of mandible	26.1	25.2 ± 0.9	24.1–26.1	5	25.0 ± 0.7	24.3–26.0	5
Height of mandible	11.4	10.9 ± 0.5	10.4–11.4	5	11.6 ± 0.3	11.1–11.8	5
Depth of mandibular ramus	5.3	5.1 ± 0.2	4.8–5.4	5	5.3 ± 0.4	4.8–5.8	5
M1 length	3.5	3.6 ± 0.1	3.4–3.7	6	3.0 ± 0.1	2.9–3.3	6
M1 width	1.9	1.8 ± 0.1	1.7–1.9	6	1.6 ± 0.1	1.5–1.6	6
M2 length	2.0	2.2 ± 0.1	2.0–2.3	6	2.0 ± 0.1	1.9–2.2	6
M2 width	1.7	1.8 ± 0.1	1.7–1.8	6	1.5 ± 0.1	1.4–1.6	6
M3 length	0.7	0.8 ± 0.1	0.7–1.0	6	0.70		2
M3 width	1.0	1.0 ± 0.1	1.0–1.1	6	0.8 ± 0.1	0.7–0.9	2
m1 length	3.3	3.3 ± 0.1	3.2–3.4	6	2.9 ± 0.1	2.8–3.0	5
m1 width	1.8	1.8 ± 0.1	1.7–1.8	6	1.5 ± 0.1	1.4–1.6	5
m2 length	2.1	2.1 ± 0.1	2.1–2.2	6	1.7 ± 0.1	1.6–1.8	5
m2 width	1.7	1.7 ± 0.1	1.7–1.8	6	1.5 ± 0.1	1.4–1.5	5
m3 length	1.0	1.0 ± 0.1	0.9–1.1	6	0.9 ± 0.1	0.8–0.9	5
m3 width	1.1	1.1 ± 0.1	1.0–1.2	6	0.9 ± 0.1	0.7–1.0	5
Head-body length	189	173 ± 11	160–190	7			
Tail length	104	98 ± 7	89–105	7			
Hind foot length	37	37 ± 1	35–39	7	36 ± 1	35–38	5
Ear length	23	22 ± 1	20–23	7			
Weight (g)	190	136 ± 35	100–190	7			

Table 1.—Extended.

Chromtomys mindorensis			*Celaenomys silaceus*					
Mean ± *SD*	Range	*n*	Mean ± *SD*	Range	*n*	*P*1	*P*2	*P*3
40.9 ± 1.0	40.1–42.8	7	37.8 ± 1.2	37.0–38.7	2	>0.50	>0.20	>0.20
14.8 ± 0.4	14.3–15.3	7	13.9 ± 0.1	13.8–14.0	2	>0.50	>0.90	>0.10
4.0 ± 0.3	3.5–4.4	7	4.2 ± 0.1	4.1–4.2	2	<0.01	>0.40	>0.50
2.2 ± 0.1	2.1–2.4	7	1.8 ± 0.2	1.7–2.0	2	>0.20	>0.10	>0.10
22.5 ± 0.6	21.9–23.5	7	20.3 ± 0.6	19.9–20.7	2	>0.50	>0.20	>0.05
15.6 ± 0.5	15.1–16.6	7	14.6 ± 0.7	14.1–15.1	2	>0.20	>0.20	>0.20
5.9 ± 0.1	5.7–6.1	7	5.0 ± 0.1	4.9–5.0	2	<0.02	>0.20	<0.001
12.5 ± 0.2	12.1–12.8	7	11.2 ± 0.4	10.9–11.4	2	<0.01	<0.01	<0.01
9.9 ± 0.3	9.5–10.4	7	9.3 ± 0.3	9.1–9.5	2	>0.10	>0.40	>0.05
12.2 ± 0.3	11.7–12.6	7	11.6 ± 0.2	11.5–11.8	2	<0.05	<0.001	>0.10
16.0 ± 0.2	15.8–16.2	7	14.8 ± 0.1	14.8–14.9	2	>0.20	>0.10	<0.001
21.6 ± 0.6	20.9–22.5	7	18.7 ± 0.4	18.4–19.0	2	>0.50	>0.50	<0.02
7.4 ± 0.3	6.9–7.7	7	6.8 ± 0.1	6.7–6.8	2	<0.001	>0.05	<0.001
13.5 ± 0.4	13.0–14.1	7	12.4 ± 0.2	12.3–12.6	2	>0.90	>0.50	>0.05
13.2 ± 0.5	12.3–14.1	7	12.2 ± 0.4	12.0–12.5	2	>0.20	>0.40	>0.10
3.9 ± 0.2	3.7–4.2	7	3.1 ± 0.1	3.0–3.2	2	>0.50	>0.10	<0.05
17.7 ± 0.5	17.3–18.7	7	16.0 ± 0.6	15.6–16.4	2	>0.50	>0.90	>0.05
8.5 ± 0.3	8.1–8.8	7	6.6 ± 0.4	6.3–6.8	2	<0.05	>0.40	<0.01
7.7 ± 0.3	7.4–8.1	7	6.3 ± 0.4	6.0–6.6	2	<0.05	>0.40	<0.02
3.0 ± 0.2	2.6–3.2	7	3.0		2	>0.90	>0.50	>0.50
6.2 ± 0.4	5.8–6.6	7	4.3 ± 0.3	4.1–4.5	2	<0.01	>0.50	<0.001
7.8 ± 0.2	7.5–8.2	7	6.2 ± 0.1	6.2–6.3	2	<0.001	<0.02	<0.001
6.5 ± 0.4	5.9–7.2	7	3.7 ± 0.4	3.4–4.0	2	<0.001	>0.50	<0.001
8.1 ± 1.3	6.6–9.6	7	9.1		1	>0.90	<0.05	>0.20
26.2 ± 0.6	25.2–26.7	7	22.1 ± 0.8	21.5–22.7	2	>0.50	<0.05	<0.01
11.9 ± 0.3	11.5–12.4	7	10.5 ± 0.3	10.3–10.7	2	<0.05	<0.01	>0.40
5.5 ± 0.2	5.1–5.7	7	4.4 ± 0.1	4.4–4.5	2	>0.50	<0.02	<0.02
3.7 ± 0.2	3.4–4.0	7	2.5		2	<0.001	>0.20	<0.001
1.9 ± 0.1	1.8–2.0	7	1.3		2	<0.001	>0.50	<0.001
2.3 ± 0.2	2.1–2.6	7	1.6 ± 0.1	1.5–1.7	2	<0.02	>0.20	<0.001
1.9 ± 0.1	1.7–2.0	7	1.2 ± 0.1	1.2–1.3	2	<0.001	<0.02	<0.001
0.8 ± 0.2	0.6–1.2	7	0.6 ± 0.1	0.5–0.6	2	>0.20	>0.90	<0.05
1.1 ± 0.1	1.0–1.3	7	0.6 ± 0.1	0.5–0.7	2	<0.01	>0.05	<0.001
3.2 ± 0.2	3.0–3.5	7	2.4 ± 0.1	2.3–2.4	2	<0.001	>0.40	<0.001
1.8 ± 0.1	1.7–2.0	7	1.2		2	<0.001	>0.20	<0.001
2.0 ± 0.1	1.9–2.2	7	1.6 ± 0.1	1.5–1.6	2	<0.001	>0.05	<0.001
1.8 ± 0.1	1.7–1.9	7	1.2 ± 0.1	1.1–1.2	2	<0.001	>0.20	<0.001
1.1 ± 0.1	1.0–1.2	7				<0.02	<0.02	
1.2 ± 0.1	1.1–1.3	7				<0.01	>0.10	
167 ± 13	155–186	5	173		1		>0.40	>0.90
112 ± 11	99–123	5	116.5		1		<0.05	<0.05
38 ± 2	36–40	6	36.7 ± 0.2	36.5–36.8	2	>0.20	>0.20	>0.50
21 ± 2	19–23	4					>0.50	
172 ± 24	152–199	3					>0.10	

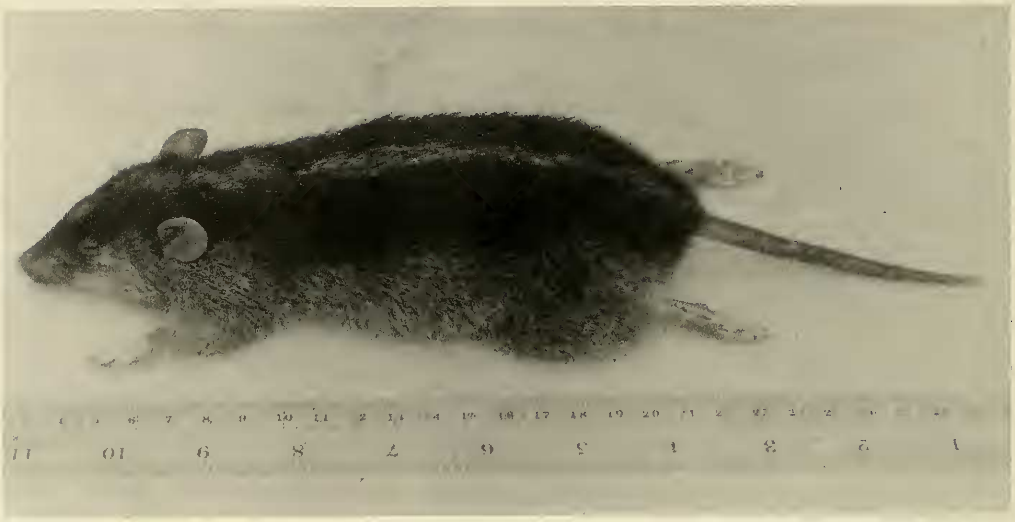

Fig. 1. Adult male *Chrotomys gonzalesi* (USNM 458952, holotype).

The plantar surface is naked, with pale gray pigmentation to the base of the toes. Four interdigital pads and one medial metatarsal pad (thenar) are well developed. A tiny lateral metatarsal pad (hypothenar) is present on five of the eight specimens (in two specimens only on one foot). Skin of the tail is pale gray dorsally, nearly white below, with a sparse covering of short blackish hairs. In some specimens the tail has a short (< 1 cm) nearly white tip. Mid-dorsal tail scales are small (16–18 rows/cm) and roughly square. Three stiff, dark gray hairs about 2 mm long are associated with each scale. Females have two inguinal pairs of mammae.

The skull (Fig. 2) is wedge-shaped and robust, with a long, tapered rostrum, an expanded interorbital region, and a narrow braincase. Supraorbital and temporal surfaces are smooth and lack ridges. Nasals are short, terminating posterior to the incisor alveoli. Premaxillaries project only slightly beyond the anterior incisor faces. The interpremaxillary foramen is greatly enlarged. Incisive foramina are short and narrow, and are intersected by the premaxillary-maxillary suture near their posterior margins. The bony palate ends medial to the anterior margin of M3. Posterior palatine foramina are positioned between M1 and M2. There is a lateral alisphenoid strut separating the accessory foramen ovale from the masticatory-buccinator foramen. The auditory bullae are small and tightly attached to the squamosal. The squamoso-mastoid foramen is small. The mandible is long and thin, with a flattened, pitted region on the lower edge immediately behind the symphysis. The root of the lower incisor extends posteriorly into the condyloid process. Upper incisors are strongly procumbent, rounded in front, and ungrooved. Incisor enamel is pale, creamy yellow, forming a thin layer confined to the anterior surface of the tooth. The first two upper molars have moderately high cusps connected to form transverse laminar ridges. M3 is reduced to a simple peg without cusp definition. Upper molars lack posterior cingula. Both m1 and m2 have small posterior cingula.

Comparisons.—Specimens of *Chrotomys gonzalesi* are much darker than any *C. mindorensis* or *C. whiteheadi* examined. The darkened areas that form two dorsal stripes on the other species are much wider, so that specimens of *C. gonzalesi* appear to be generally blackish above, as opposed to predominantly brown or tan with a pair of nar-

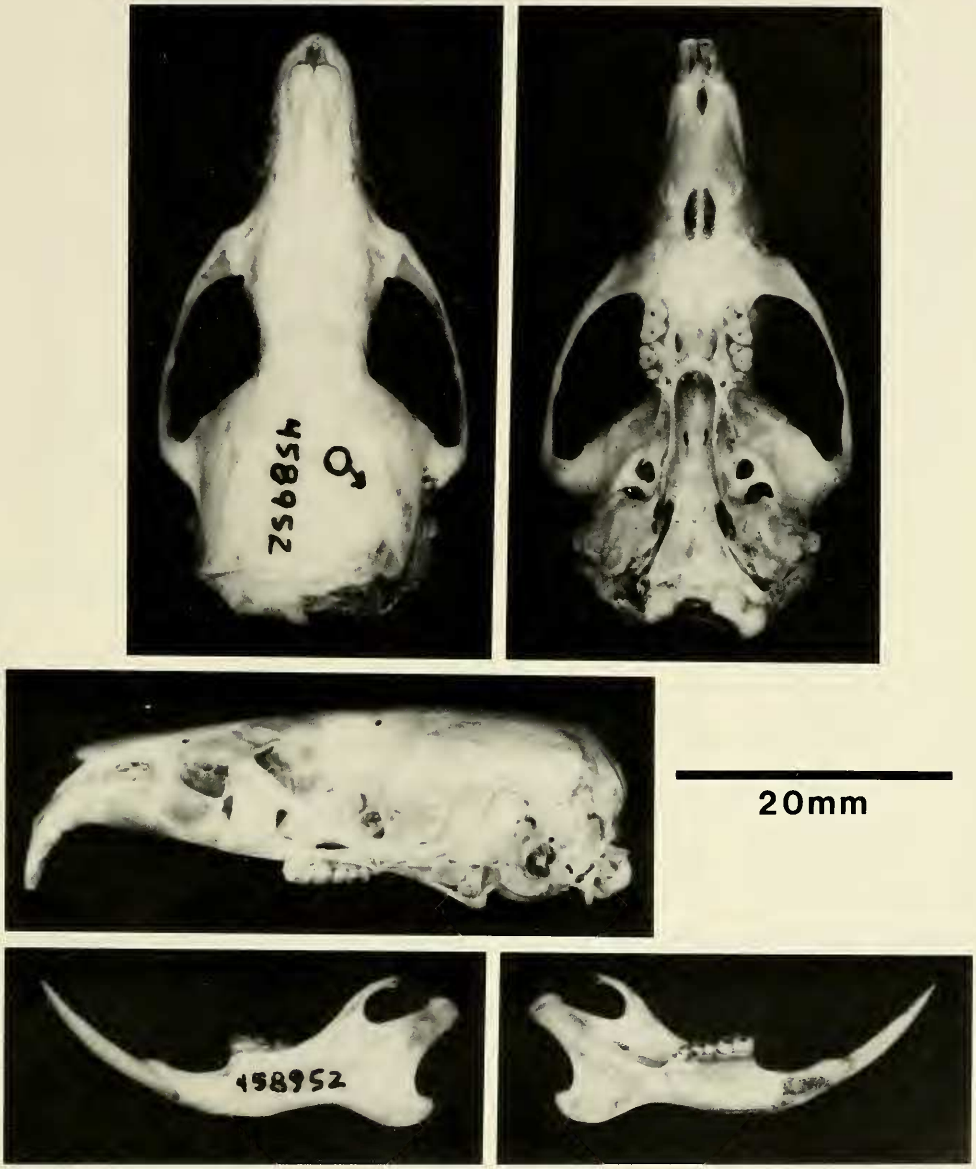

Fig. 2. Dorsal, ventral, and lateral views of cranium, and labial and lingual views of left mandible of *Chrotomys gonzalesi* (USNM 458952, holotype).

row black stripes (Musser et al. 1982). The blackish dorsal aspect of *Chrotomys gonzalesi* also differs from *Celaenomys,* which is dark gray with faint brown highlights, and is marked dorsally with a pale blaze on the forehead and (in some specimens) a faint line over shoulders. As in the other species of *Chrotomys, C. gonzalesi* has a pale mid-dorsal stripe. In some specimens, the narrow stripe extends from the forehead to the base of the tail, a configuration similar to that of *C. whiteheadi,* but different from the broader stripe of *C. mindorensis.* In other specimens the mid-dorsal stripe is faint and discontinuous. Lateral color is yellowish buff, similar to that of *C. mindorensis* but different from the pale brown of *C. whiteheadi.* The pale lateral region is less extensive than in the other *Chrotomys* species. Underparts also are darker than in other species. Pelage of the new species is soft, dense, and long like that of *C. whiteheadi,* but different from the thinner and harsher pelage of *C. mindorensis* (Musser et al. 1982). The pelage of *Celaenomys* is softer, thicker, and shorter than that of *Chrotomys gonzalesi.* The tail of *C. gonzalesi* has pale gray scales with dark hairs as opposed to the brownish or brownish black scales with silvery hairs in the other species.

Body size is similar in all four species. The tail of *Chrotomys gonzalesi* is both proportionately and absolutely shorter than in either *Chrotomys mindorensis* or *Celaenomys silaceus* (Table 1). Tail length averages 56.5% (54.8–60.0%) of head-body length compared to 67.1% (56.9–76.4%) in *C. mindorensis* and 67.3% for one specimen of *Celaenomys.* Available specimens of *Chrotomys whiteheadi* lack external measurements; however, the skins appear to have relatively short tails. Measurements reported by Thomas (1895) for the holotype indicate a proportionate length of 56.6%, near the mean value for *C. gonzalesi* but below the range for *C. mindorensis.* Plantar pads of *Chrotomys gonzalesi* are substantially smaller than those on fluid-preserved specimens of *C. mindorensis.* The lateral metatarsal pad (hypothenar) is either rudimentary (five specimens) or absent (three specimens) in *C. gonzalesi,* whereas it is well developed in *C. mindorensis.* The plantar pads of both *Chrotomys whiteheadi* and *Celaenomys silaceus* have the same general arrangement, but their comparative size and the frequency of occurrence of the hypothenar cannot be determined from available material (no fluid-preserved specimens are known to us).

Cranial structure of *Chrotomys gonzalesi* is similar to that of the other members of the genus and to *Celaenomys.* However, there are significant differences between species for many measurements (Table 1). The skull of *Chrotomys gonzalesi* is larger than that of *Celaenomys,* with broader braincase, palate, mastoid region, interorbital region, and zygomatic arches, broader and deeper rostrum, and larger auditory bullae. In comparison to the other *Chrotomys* species, *C. gonzalesi* has a lower braincase, broader mastoid region, and wider bony palate. From *C. whiteheadi* it is further distinguished by its shorter incisive foramina, larger auditory bullae, broader interorbital region, and both broader and deeper rostrum (Table 1). The postglenoid vacuity between the auditory bulla and the squamosal bone is small in all three *Chrotomys* species, but is large in *Celaenomys.* Aside from this, no consistent differences among species in the size or positioning of cranial foramina were noted. The mandible of *Chrotomys gonzalesi* is similar to that of *C. whiteheadi,* but shorter and thinner than that of *C. mindorensis,* and longer and thicker than that of *Celaenomys.* Posterior height of the mandible is less than in the other species of *Chrotomys.* The exposed portion of the lower incisor is longer in *C. gonzalesi* and *C. whiteheadi* than in *C. mindorensis.* Although cheekteeth of all four species exhibit the same general cusp pattern, there are substantial differences in size. Molars of *C. gonzalesi* are nearly the same size as those of *C. mindorensis,* but are larger than those of both *C. whiteheadi* and *Celaenomys.*

A principal components analysis based on 14 cranial and mandibular measurements (Table 2) was conducted on a subset of 15 specimens on which all measurements could be taken. The first three components account for 85% of total variation. The first component, accounting for 58% of the variation, shows positive loadings of similar magnitude for most variables, indicating that it is primarily size that is represented. *Celaenomys* is distinguished from *Chrotomys* by low scores on this axis (Fig. 3), reflecting its smaller size.

Table 2.—Character loadings on first three components of principal components analysis using log-transformed cranial and mandibular measurements of 15 adult *Chrotomys* and *Celaenomys.*

Character	Component		
	1	2	3
Diastema length	0.249	0.364	0.282
Incisive foramina length	−0.042	0.283	0.552
Palatal length	0.308	0.254	0.013
Length of bulla	0.310	−0.188	−0.084
Height of braincase	0.148	0.182	−0.642
Interorbital breadth	0.245	−0.309	0.258
Length of rostrum	0.323	0.173	0.145
Depth of rostrum	0.333	−0.119	0.028
Zygomatic plate breadth	0.070	0.443	0.084
Maxillary toothrow	0.307	−0.272	−0.007
Palatal breadth	0.305	−0.250	0.157
Mandibular toothrow	0.314	−0.229	0.022
Mandible height	0.262	0.298	−0.238
Mandibular ramus	0.296	0.202	−0.135
Eigenvalue	8.131	2.248	1.565
Variance explained	58.1%	16.0%	11.2%

Component two (accounting for an additional 16% of total variation) contrasts individuals with long diastemas, incisive foramina, and bony palates, deep braincases and mandibles, narrow interorbital regions and bony palates, broad zygomatic plates, and short toothrows against individuals having the converse. Specimens of *Chrotomys whiteheadi* score high on this axis, those of *C. gonzalesi* and *C. mindorensis* score low, and those of *Celaenomys* are intermediate (Fig. 3). Component three (accounting for 11% of the variation) primarily contrasts individuals with long diastemas and incisive foramina, and shallow braincases against individuals with the converse. *Chrotomys gonzalesi* and *C. whiteheadi* have high scores, whereas *C. mindorensis* and *Celaenomys* have low scores on this axis (Fig. 3). All four taxa are fully separated from the others along at least one axis. There also is extensive overlap among *C. mindorensis* from Mindoro and Luzon, supporting the conclusion of Musser et al. (1982) that populations from the two islands are conspecific.

Ecology.—*Chrotomys gonzalesi* apparently is restricted to montane and "mossy" forest habitats (lower and upper montane rain forest habitats, sensu Whitmore 1984) above 1350 m elevation (Rickart et al. 1991). These habitats are characterized by a cool and wet climate year-round, steep slopes, and woody vegetation dominated by species in the families Fagaceae and Lauraceae (as opposed to the Dipterocarpaceae of lowland forests). The forest canopy varies from low (5 m) to moderate (20 m) and at higher elevations is broken by numerous treefalls. Vascular epiphytes and vines are abundant and the soil has a thick layer of humus. At 1750 m, thick layers of mosses and liverworts cover most subcanopy surfaces. Mosses are less common at 1350 m (Goodman & Gonzales 1990, Rickart et al. 1991).

Trapping data indicate that *C. gonzalesi* is uncommon where it occurs. In 4900 trap nights at sites at or above 1350 m, only eight specimens were obtained. In a comparable effort at lower elevations on Mount Isarog (4101 trap nights), no specimens were caught. Specimens were taken in Victor rat traps (seven animals) and a National live trap (one animal) set on the ground in areas

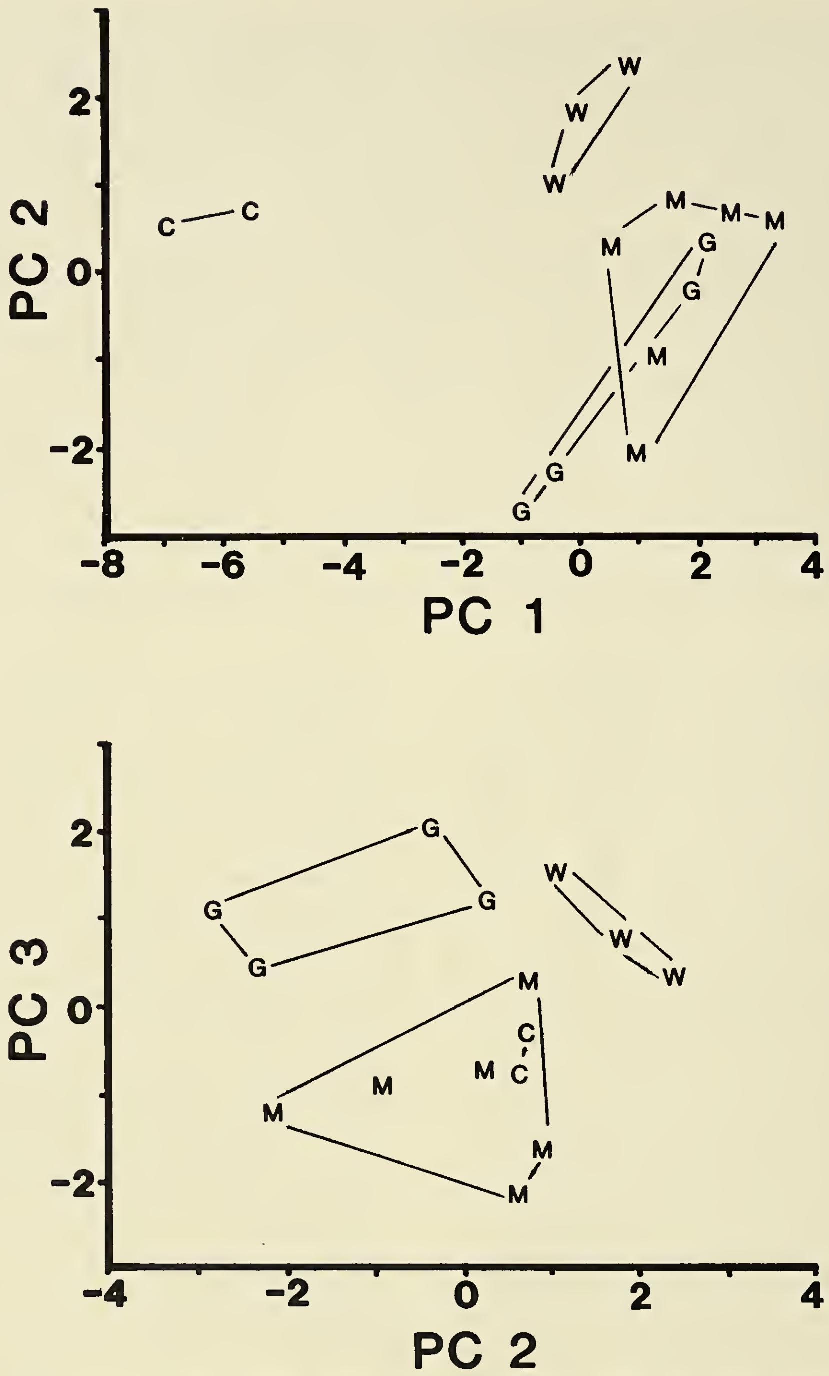

Fig. 3. Results of principal-component analysis of 14 cranial and mandibular measurements; scores for individual specimens are plotted on components 1 and 2 (top) and components 2 and 3 (bottom). C = *Celaenomys silaceus*, G = *Chrotomys gonzalesi*, M = *C. mindorensis*, and W = *C. whiteheadi*.

of heavy cover. Most individuals were caught along runways by fallen logs or in subsurface openings among exposed tree roots. Six animals were caught in traps baited with annelid worms, and two were taken in traps baited with fried coconut coated with peanut butter. Stomach contents of five snap-trapped specimens included (in order of decreasing frequency) remains of earthworms (Annelida: Megascolecidae), small terrestrial amphipods (Amphipoda), insect larvae (Coleoptera and Diptera), adult insects (Orthoptera and Diptera), and spiders (Araneida). None contained identifiable plant matter. Three individuals were trapped during daylight hours, one was caught at dusk, and four were trapped at night. Other small mammals trapped in close association with *Chrotomys gonzalesi* were *Crocidura grayi, Apomys musculus, Apomys* cf. *microdon, Archboldomys luzonensis,* an undetermined species of *Batomys, Rattus everetti,* and *Rhynchomys isarogensis* (Rickart et al. 1991).

Reproductive activity of *Chrotomys gonzalesi* was evident during the three months of field work. An adult female taken on 20 March had prominent teats and five placental scars (probably two sets). An adult female taken on 27 April contained two embryos in early development. Adult males trapped on 27 March and 28 April were in full breeding condition (scrotal testes, convoluted epididymides). Immature animals were caught in late March. A pregnant female and adult male were taken in the same trap on consecutive nights.

Discussion

Evidence from morphology, stomach contents, and trapping results indicates that *Chrotomys gonzalesi* is a semifossorial, primarily vermivorous species active day and night (Rickart et al. 1991). Presence of a pregnant female at the end of April and large immature animals in March suggests that the breeding season is relatively long. There is little information on ecology of the nearest relatives of *C. gonzalesi. Chrotomys whiteheadi* and *Celaenomys silaceus* occur in montane forest in the highlands of northern Luzon. The former includes earthworms in its diet and probably is ecologically similar to *C. gonzalesi* (Rabor 1955, Sanborn 1952). *Chrotomys mindorensis* occurs in a variety of lowland habitats in central Luzon and southwestern Mindoro (Barbehenn et al. 1973, Temme 1974); habitat differences suggest that it is ecologically distinct from the other species.

The discovery of *Chrotomys gonzalesi* supports the pattern of vicariant speciation between northern and southern Luzon that was postulated by Musser & Freeman (1981) on the basis of their description of *Rhynchomys isarogensis.* Both *Chrotomys gonzalesi* and *Rhynchomys isarogensis* apparently are restricted to high elevation forest on Mount Isarog, a habitat pattern shared with two other murid species endemic to the mountain (*Archboldomys luzonensis* and *Batomys* sp.). Extensive lowlands separate the highland forests of Mount Isarog from similar areas in northern Luzon that support *Chrotomys whiteheadi* and *Rhynchomys soricoides.* The mountain also is distant from the range of *Chrotomys mindorensis,* not known to occur south of Laguna Province (ca. 250 km WNW of Mount Isarog). During Pleistocene glacial periods when sea level was low and temperatures cooler (Heaney 1986, Heaney & Rickart 1990), montane forest probably extended further down into lowland regions allowing contact between populations now geographically and ecologically isolated (Musser & Freeman 1981). The rich endemic mammal fauna of Mount Isarog suggests that the Camarines Peninsula has experienced long periods of relative isolation from the main Luzon land mass. In this light, further studies of the murids of southern Luzon (including *Apomys, Batomys,* and *Phloeomys*) would be of interest, and a survey of other highland areas on the peninsula, particularly Mount

Bulusan (1559 m) at the southernmost tip of Luzon, would be informative.

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